

LIFE HISTORY OF *EUTRETA DIANA* (OSTEN SACKEN) ON
ARTEMISIA TRIDENTATA NUTTALL IN
SOUTHERN CALIFORNIA (DIPTERA: TEPHRITIDAE)

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Abstract.—*Eutreta diana* (Osten Sacken) is univoltine on *Artemisia tridentata* Nuttall (Asteraceae), its only reported host plant in southern California. Eggs are inserted in axillary and terminal buds on young branches in late spring. First instars diapause, and gall growth essentially ceases, for the next six or seven months until larvae molt and then overwinter as second instars in very small galls. Branch elongation and gall and larval growth resume in spring. Galls are described in detail and pictured. Pupation and adult emergence occur mainly in April and early May. Newly emerged females require two to three weeks to mature eggs, mate, and begin oviposition.

Principal natural enemies of *E. diana* include the parasitoids, *Eurytoma* sp. and *Rileya* sp. (Eurytomidae), *Pteromalus* sp. (Pteromalidae), *Tetrastichus* sp. (Eulophidae), and *Torymus citripes* (Hüber) (Torymidae), and avian bushtits, *Psaltriparus* sp., besides arthropod predators and other mortality factors identified.

Key Words.—Insecta, *Eutreta*, *Artemisia*, gall, parasitoids, life history, predation, larval morphology

Live specimens of *Eutreta diana* (Osten Sacken), with their pale green eyes, white-dotted black wings, and bright red abdomens, represent one of the more beautiful species of fruit flies (Diptera: Tephritidae) in California. This aesthetic consideration, plus my discovery of several field populations of *E. diana*, provided me with ample reasons to study its life history.

Taxonomy.—First described as *Trypeta diana* by Osten Sacken (1877), *Eutreta diana* and two separately described color variants of the adults were synonymized by Stoltzfus (1977), who also illustrated the adults in his comprehensive revision of the genus. Second and third instars and the puparium of *E. diana* were described and illustrated by Steck & Wharton (1986).

Distribution, Hosts and Study Sites.—Stoltzfus (1977) mapped the North American distribution of *E. diana* as California, Oregon, and Washington east into the Dakotas, Nebraska, Colorado, and New Mexico, and adjacent parts of Canada and Baja California, Mexico. Benbow & Foster (1982) also reported this fly from northwestern Texas and called it “one of the most widely encountered gall-forming tephritids in western North America.” Foote & Blanc (1963) and Stoltzfus (1977) noted that it has been collected as far east as Missouri, well east of the distribution actually mapped by the latter author, who also suggested that its southern distribution extends into Mexico, presumably meaning east of Baja California. Foote & Blanc (1963) plotted the distribution of *E. diana* in northern California along the length of the northern and central Sierra Nevada Mountains, and in southern California, from the Palomar, Cuyamaca, and Laguna Mountains in Riverside and San Diego Counties southwest to the Pacific Coast.

My field-study locations for flies and galls on *Artemisia tridentata* Nuttall (Asteraceae) in the southern Sierra Nevada and San Bernardino Mountains serve to

connect the apparent northern and southern segments of its California distribution: Horse Meadow, 2225 m, Mahogany Creek, and Taylor Creek, Sequoia National Forest (northern section), Tulare Co., 1985 and 1986, and Mormon Rocks, Cajon Pass, San Bernardino National Forest, San Bernardino Co., 1986–1989. Additional locations where the characteristic galls on *A. tridentata* were observed or collected included: Rattlesnake Creek above S. Fork of Santa Ana River, San Bernardino Mts., San Bernardino National Forest, San Bernardino Co., 9 Jun 1981; Mojave River Forks, 975 m, San Bernardino National Forest, San Bernardino Co., 22 Apr 1986. Adults were also swept as follows: road to Horseshoe Meadow, 2750 m, Inyo National Forest, Inyo Co., 22 Jul 1987; White Mountain, 3150 m, Inyo National Forest, Inyo Co., 19 Aug 1987. Unless otherwise stated, most of the observations were made at the Mormon Rocks site.

The recorded hosts of *E. diana* include six species and two varieties of *Artemisia* representing tall and erect as well as low-growing shrubs (Fronk et al. 1964, Stoltzfus 1977, Benbow & Foster 1982).

Egg.—No intact egg was found in nature because they are inserted for most of their length tightly into buds, cannot readily be seen with the naked eye, and are easily overlooked and destroyed even during dissection under a stereomicroscope. Three ova dissected from a sexually mature, field-collected female were fusiform, smooth, white, bluntly rounded at both ends, 0.55 mm long and 0.25 mm wide, and at the cephalic end bore a 0.06 mm, peg-like pedicel. Within a bud, an egg was surrounded by brown necrotic tissue.

Larva.—Eclosion was not studied, except to note that an embryo had rotated 180° before hatching. Upon hatching, first instars tunneled basipetally into the pith but moved only 2 to 3 mm during the six to seven months following oviposition, which mainly took place in May 1987. The first instar is 1.1–1.2 mm long and is easily distinguished by its red-brown cephalopharyngeal skeleton and a black patch of verrucae on the abdominal ventor (Fig. 1a).

Examination of this instar by scanning electron microscopy (see Headrick & Goeden in press for materials and methods) determined that the verrucae actually ringed several abdominal segments (II–V dorsally, Fig. 2a; I–VII ventrally, Fig. 2b), but only the central portion of the ventral verrucae were pigmented (Figs. 2a, 2b). Two forms of verrucae were seen at higher magnification (Fig. 2c); the larger morphs are less common, unevenly distributed, and have a central pore. The dark ventral verrucae are less scattered than the lateral and dorsal verrucae, being aligned in transverse rows (Fig. 2d).

The function of the segmental verrucae is uncertain, but an ambulatory role is probable, although the larva could move little in its confined quarters. Like the cephalopharyngeal skeleton, the patch appeared to darken as the first instar aged, but was absent, or at least not prominent on the second and third instars. Furthermore, no such patch was mentioned by Steck & Wharton (1986) in their detailed descriptions of the last two instars.

Thirty-one small and barely recognizable bud galls were collected on 9 Nov 1988, at the beginning of overwintering by *E. diana*. These young galls were merely slightly clavoidal swellings of the distal parts of lateral and terminal vegetative branches (Fig. 1b). Twenty-one (68%) of the 31 galls contained live first instars; seven had begun to molt, indicating the second instar served as the main overwintering stage. The 21 galls with live larvae averaged 1.89 ± 0.06 ($\bar{x} \pm SE$)

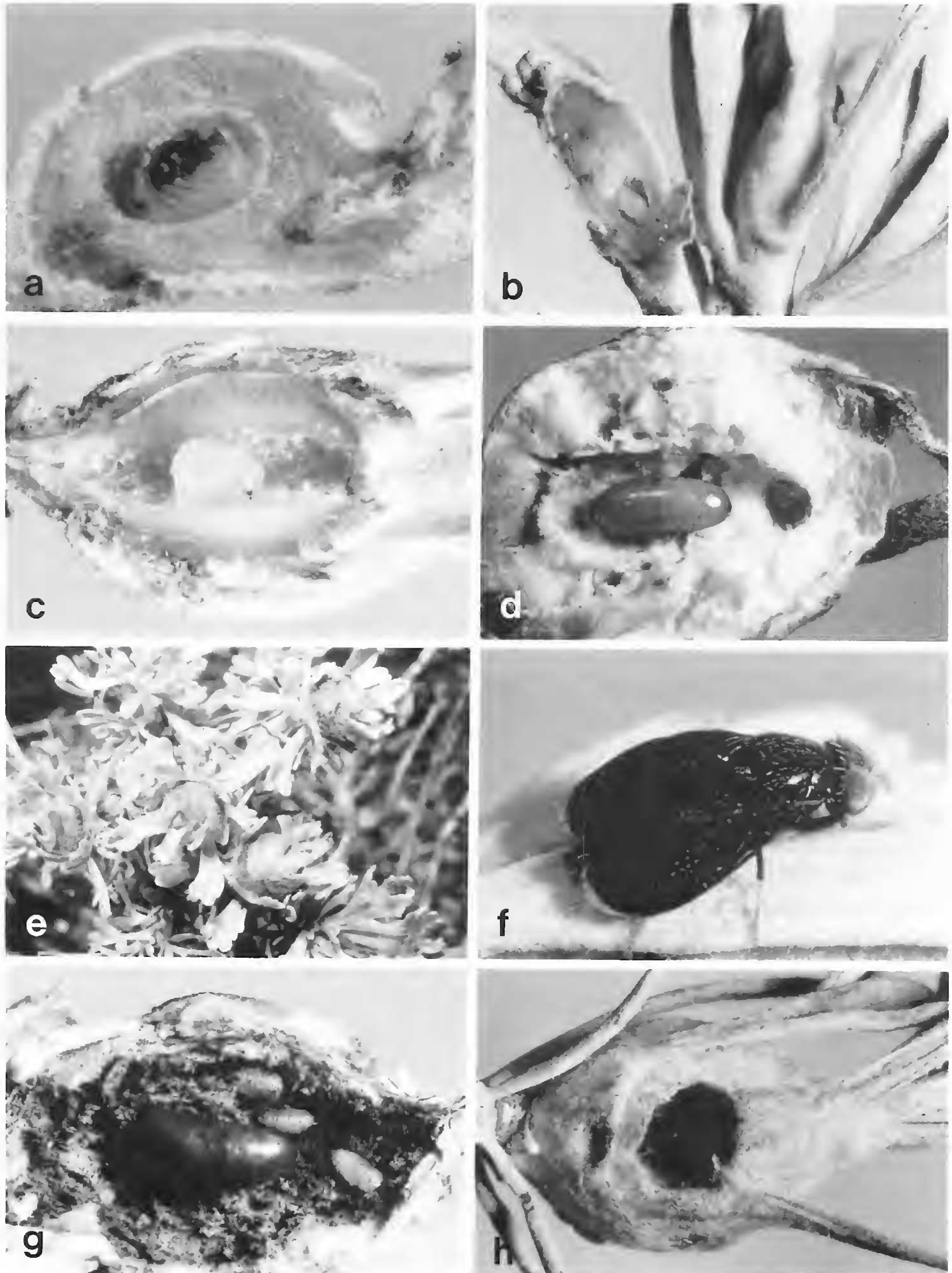


Figure 1. Life stages and galls of *Eutreta diana* on *Artemisia tridentata*: (a) first instar in small gall (note black verrucae on ventor) ($15\times$); (b) dissected (left) and intact (right) small galls contained first instars ($5\times$); (c) overwintered second instar in gall ($11\times$); (d) puparium in central cavity with exit tunnel and exit hole to right (note tunnels of agromyzid larvae in walls) ($4\times$); (e) mature galls ($0.8\times$); (f) female at rest ($8\times$); (g) puparia of *E. diana* and *Liriomyza* sp. in gall heavily mined by the latter ($5\times$); (h) gall with hole through which bushtit extracted larva ($4\times$).

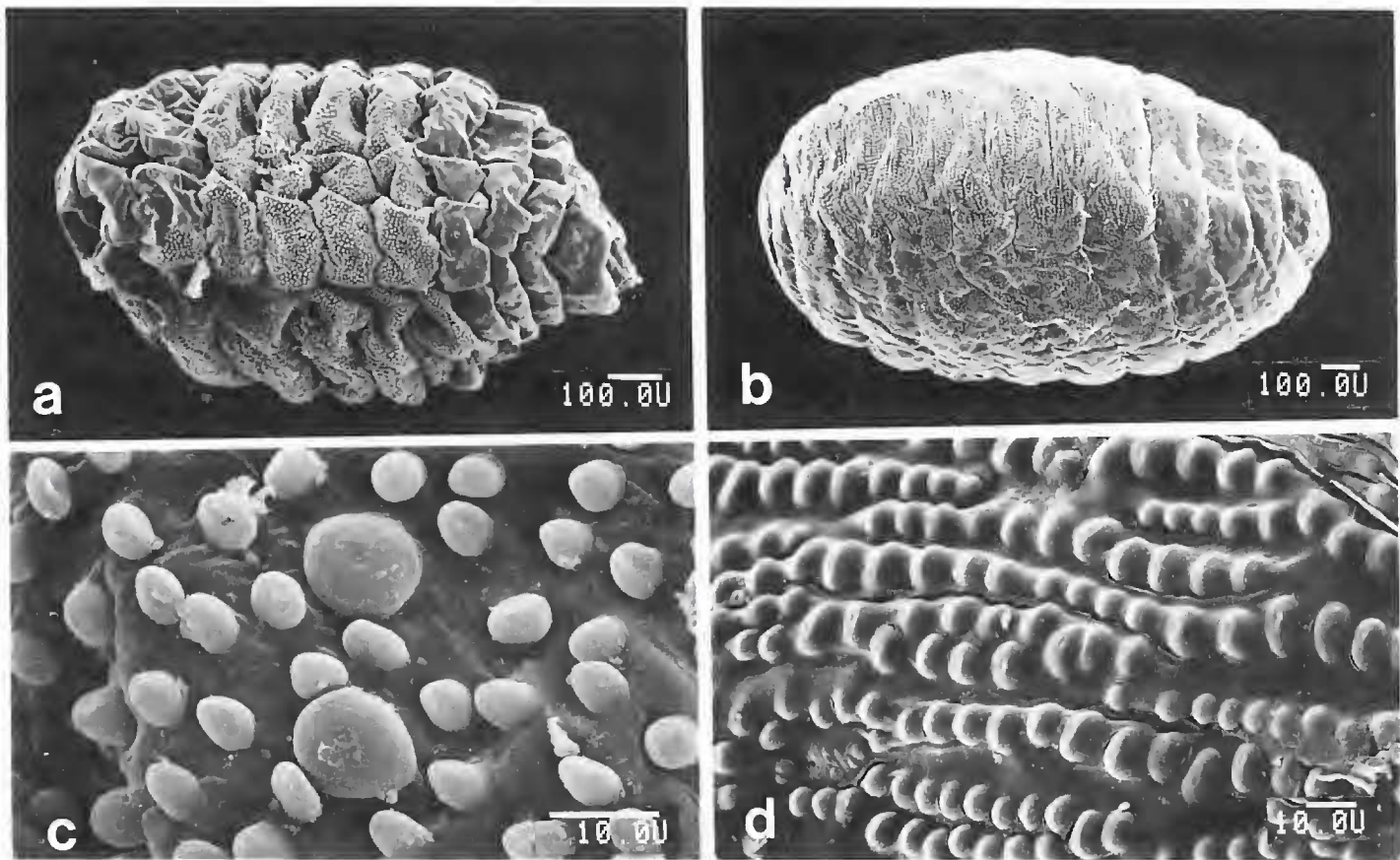


Figure 2. First instar *Eutreta diana*: (a) lateral view; (b) ventral view; (c) detail of two morphs of verrucae; (d) detail of ventral verrucae (pigmented).

(1.87–2.55) mm in diameter, measured at the level of the gall cavities, and 2.03 ± 0.06 (1.50–2.57) mm at their maximal width slightly more distally. Benbow & Foster (1982) reported that galls of *E. diana* on *A. filifolia* Torrey containing first instars averaged 8 mm in diameter only a month or so after eclosion. The cavities within the young galls from Mormon Rocks ended an average of 2.51 ± 0.17 mm from the gall apices (Fig. 1a) and were ellipsoidal, frass-free, open, and smooth-surfaced; they averaged 0.97 ± 0.03 mm in diameter and were 1.56 ± 0.07 mm long. The thickness of gall walls varied from 0.2–0.6 mm. Ten of the 31 first instars examined were dead, and on one of these a parasitoid adult developed (identified below).

On 21 May 1986, just after snow melt allowed access to the Horse Meadow site (2225 m), 122 overwintered galls were collected, refrigerated, and dissected in the laboratory during the next week. Only one gall showed little growth, measured 6 mm long by 3 mm wide, and contained a live early second instar in a 2 mm long, 0.5 mm wide cell. This may typify the overwintering state. This gall sample also contained 44 (36%) more advanced second instars (Fig. 1c), 21 (17%) of which had been killed by parasitoids or unknown causes. In the 21 galls containing dead larvae, the cavities had become wholly or partly filled with the enlarged parenchymatous pith cells constituting most of the gall tissue, and which the larvae rasp with their mouth-hooks while feeding. The 23 (19%) subspheroidal galls that contained actively feeding or molting second instars averaged 8.7 ± 0.4 mm long by 7.5 ± 0.3 mm wide. These lively larvae occupied open, approximately 1 mm wide, central-longitudinal feeding chambers which also contained a small accumulation of whitish frass (Fig. 1c). No solid feces littered the gall cavities. After molting, the exuvium and cephalopharyngeal skeleton were discarded, usually at the base of the feeding chamber. Even at this early date the remaining galls

in this sample contained two live third instars and 22 puparia, so larval development progressed at different rates even in galls along the same branch.

A sample of 92 galls collected at Taylor Creek (2072 m) on 22 May 1986 contained only three (3%) second instars, 39 (42%) third instars, and 50 (54%) puparia in contrast to the Horse Meadow sample. Earlier development by *E. diana* at low elevations was further suggested by a sample of 55 galls collected for dissection at Mormon Rocks (1017 m) on 18 May 1987. This sample contained no larvae, only three (5%) intact puparia that probably were parasitized, and 18 (33%) empty puparia from which adults already had emerged. The remaining galls bore evidence of bird predation or larval parasitism (see below).

Most larval growth takes place during the third stadium. Although Benbow & Foster (1982) stated that gall growth ceased if the larva died before it reached the third instar, my data, like their graphed mean gall diameters, suggested that gall growth continued during the third stadium. One hundred mature galls that each bore a puparium (Fig. 1d) averaged 12.0 ± 0.4 (6–19) mm in length and 10.0 ± 0.2 (6–13) mm in maximal width. The central cavities within these mature galls averaged 7.5 ± 0.2 (5–10) mm in length and 3.1 ± 0.1 (2–4) mm in width. The cavities usually were mostly frass-free, circular in cross-section, rounded basally, and smooth-walled. The thickness of galls walls varied from 1.5–4 mm.

Externally, mature galls that contained live puparia usually were subspheroidal (Figs. 1d, 1e). This gall shape also resulted when larval feeding or exit hole construction destroyed the terminal bud at the apex of a gall. Upon death or removal of a larva, or after emergence of the adult, apical growth and internode elongation usually resume and the gall assumes a spindle-shape. This causal relation for branch-gall shape was reported for other tephritids (*Trupanea conjuncta* [Adams]: Goeden 1987, *Tephritis stigmatica* [Coquillett]: Goeden 1988), as well as for a gallicolous moth (*Carolella beevorana* Comstock, Cochylidae: Goeden & Ricker 1981). Though apparently fairly common among branch-gall-forming Tephritidae, this relationship is not widely recognized (Freidberg 1984). Thus, the gall of *E. diana* is a modified branch composed of shortened and inflated internodes (Fig. 1e). The galls are grey-green when young, sometimes purple-tinted, especially when infested by inquilines and certain parasitoids (see below), but turn brown and woody with age. They are covered with a closely appressed whitish tomentum when young and are laterally marked by transverse, scale-like expanded leaf bases bearing sessile leaves and axillary buds that may grow into one or more branches adorning old empty galls. Empty galls of the current season end in clusters of leaves or a terminal branch, depending on whether the apical bud has been killed. Galls formed from axillary buds may be sessile or borne on pedicels of various lengths, whereas galls of apical buds of main branches may have pedicels several cm long. For example, 11 (37%) of 30 galls sampled at Mahogany Creek on 13 Jun 1985 were sessile but the remainder were borne on pedicels from 1–13 mm long. Similarly, 19 (50%) of 38 galls from Taylor Creek on 12 Jun 1985 were sessile although the remainder had pedicels which varied from 1–9 mm long.

Usually only a single larva of *E. diana* inhabits each gall. One gall, however, collected at Mormon Rocks on 20 May 1987 contained two intact puparia formed in separate chambers. These puparia did not yield flies or adult parasitoids when caged at room temperature in a humidity chamber. This is a rare example of a monothalmus tephritid producing a biloculate, polythalmous gall (Freidberg 1984).

Two dead second instars found within a single chamber in a gall collected at Taylor Creek on 12 Jun 1985 apparently wounded and killed each other, providing another outcome to abnormal multiple oviposition in a single bud or branch tip.

Freidberg (1984) reported that the highest record for the number of tephritid galls on a single plant probably was the 135 galls of *Spathulina sicula* Rodani he counted in Israel. I removed and counted 147 current season galls of *E. diana* from a single plant at Mormon Rocks on 27 May 1987. However, Dodson (1987) noted "over 2000" galls of *Aciurina bigeloviae* (Cockerell) reported from a 1 m diameter *Chrysothamnus nauseosus* (Pallen) Britton.

Toward the end of their feeding period, the third instars usually extended their feeding chambers distilaterally to form a curved exit tunnel. This narrowed to a 1.5 to 2 mm diameter, circular window formed by a thin layer of epidermis that is usually not visible externally when intact (Fig. 1d). A few exit tunnels projected straight outward and destroyed the apical bud. One gall was observed in which the exit tunnel had been formed basilaterally near the juncture with the pedicel. Pupariation often occurs with the anterior end of the puparium projecting into the mouth of the exit tunnel.

Pupa.—The puparium description of Steck & Wharton (1986) was based on eight specimens from California. The 40 puparia I measured (Fig. 1d) averaged 4.2 ± 0.1 (3.3–5.0) mm in length and 1.7 ± 0.1 (1.0–2.5) mm in width. These dimensions compare favorably with the 2.8–4.8 mm lengths and 1.0–1.8 mm widths reported by Steck & Wharton (1986). The puparia I examined were translucent and changed from mustard-yellow to ochrous tan with age. The abdomen eventually appeared red-brown and the rest of the body dark brown through the puparium just before adult emergence.

Adult.—Adults (Fig. 1f) were uncommon, but when found they were always on gall-bearing *A. tridentata*. The ability of *E. diana* adults to feign death and drop to the ground when disturbed reported by Steck (in Freidberg 1984) was not observed. Both sexes exhibited the alternate and synchronous wing-waving behavior described for other nonfrugivorous tephritids (e.g., *Trupanea bisetosa* [Coquillett]; Cavender & Goeden 1982, *Neotephritis finalis* [Loew]; Goeden et al. 1987, *Paracantha gentilis* Hering; Headrick & Goeden, unpublished data).

Adult emergence began approximately on 6 May 1987 as judged from emergence records for flies reared from larvae and puparia dissected from galls collected at Mormon Rocks on 30 Apr. Thirty-two males (63%) and 21 females were reared from all galls sampled in 1985; 23 males (64%) and 13 females, from galls sampled in 1986. Both sexes emerged over week-long emergence periods during both years. Newly emerged females ($n = 3$) possessed immature ovaries. Weekly dissection of three females, each held at room temperature (21° C) in separate cages and supplied with water and honey, showed that they contained full size ova between two and three weeks after emergence.

Gall-bearing plants are attacked year after year as reported by Benbow & Foster (1982), although why a plant is attacked for the first time remains unanswered (Freidberg 1984). Adults continued to frequent the plant from which I had removed all galls of the current season. The only occurrence in common that I found was that galled plants always had access to a good supply of ground water (e.g., in a wash at Mormon Rocks or other drainage at Mojave River Forks), were on the margin of a meadow (Horse Meadow), or above a running stream (Ma-

hogany Creek, Taylor Creek). Plants with galls of *E. diana* also bore galls of one or more species of Cecidomyiidae, as noted on *A. tridentata* in Wyoming (Fronk et al. 1964). Adults of *E. diana* appeared early in the year when night temperatures were low and days remained cool. Their morning activities mainly consisted of sunning to gain heat with their black bodies and dark wing color. Flies rested with their long axis perpendicular to, and dorsa facing, the sun and with their wings held flat, motionless, and parted (Fig. 1f). Their characteristic dark wings no doubt function in heat gain, raising body temperature to facilitate early daytime and seasonal activities at higher altitudes.

Mating was observed once, at 08:15 h on 9 Jun 1987. Although the start and finish of this single act of copulation was not observed, the flies were initially located on the underside of a vertically oriented leaf. The male was positioned over the posterior of the thorax and the abdomen of the female with his wings motionless and straight back but overlapping and flat upon his dorsum. The wings of the female were slightly parted and also motionless. The male was held off the substrate and carried by the female as she alternately walked or rested, as they pumped their mouthparts and remained in copula.

Oviposition by a single female was observed between 13:30–14:00 h on 27 May 1987. She backed into, and oviposited directly into, two axillary buds, while probing other buds for 15–20 sec each without ovipositing. The two acts of oviposition lasted 3:50 min and 3:45 min, and were subsequently confirmed by observing the eggs in the excised buds after dissection under a stereomicroscope.

Phenology.—Adult emergence and activity coincided with flowering by *Yucca whipplei* Torrey (Agavaceae) and *Eriodictyon crassifolium* Benth (Hydrophyllaceae) at the Mormon Rocks site. The adults disappeared about the time that *Senecio douglasii* deCandolle began to bloom there in 1986 and 1987.

Seasonal History.—*Eutreta diana* is univoltine on *A. tridentata* in southern California, although it might be able to produce additional generations on one or more alternate but as yet undetected hosts (Foote & Blanc 1963, Wasbauer 1972), as predicted by host records from Wyoming (Fronk et al. 1964) and Texas (Benbow & Foster 1982). Two of the four alternate hosts, *A. arbuscula* Nuttall and *A. cana* Pursh, reported by Fronk et al. (1964) also occur in northern California (Munz & Keck 1959), but not in southern California (Munz 1974) where these studies were conducted. I have reared *E. simplex* Thomas from galls on a different species of *Artemisia* (unpublished data), but not *E. diana*. My sweep records of live adults from high elevations in July and August also indicate that alternate hosts are present in California.

The biology and seasonal history of *E. diana* on *A. filifolia* in Texas (Benbow & Foster 1982) is very different than on *A. tridentata* in southern California. Both populations appear to be univoltine. The overwintering stage is the egg in Texas, but mainly the second instar in southern California. First instars hatch in late March to mid-April in Texas, where the first stadium lasts approximately a month, in contrast to the six or seven months in southern California! Subsequent larval and gall growth are continuous in Texas, without summer and fall diapause by the first instar and concomitant arrested gall development that is now known from southern California. Pupation occurs in late August to early September in Texas and lasts about a month, whereas, in southern California it occurs in late

spring (April and May) and lasts about two weeks. Adults emerged in the fall to oviposit the overwintering eggs in Texas, but emerged and oviposited in late spring in southern California. Life history differences of this magnitude suggest that Texas and California populations may be temporally, spatially, and ethologically separated by their different host plant affinities and therefore possibly sibling species which should undergo morphological re-examination. Stoltzfus (1977) recognized great variability in the color of *E. diana* adults.

Natural Enemies and Inquilines. — The larvae were heavily parasitized by Hymenoptera including: *Eupelmus* sp. (Eupelmidae), a solitary, ectoparasitoid of the first instar; *Pteromalus* sp. (Pteromalidae), a solitary, larval ectoparasitoid; *Eurytoma* sp. and *Rileya* sp. (Eurytomidae), solitary, larval, endoparasitoids; *Tetrastichus* sp. (Eulophidae), a gregarious, larval-pupal endoparasitoid; and *Torymus citripes* (Hüber) (Torymidae), a solitary, larval, ectoparasitoid. These parasitoids were reared from isolated parasitized hosts (humidity chamber). The latter species killed and devoured the young larvae of *E. diana*, and then completed its development by tunneling in the walls of the gall. This same behavior was ascribed to a *Eurytoma* sp. by Benbow & Foster (1982), who reared an additional five species of parasitic Hymenoptera from galls of *E. diana* in Texas, including a *Tetrastichus* sp. Fronk et al. (1964) also reported a braconid (*Dacnusa* sp.) as a parasitoid of *E. diana*.

Larvae of *Apion* sp. (Coleoptera: Apionidae) and an unidentified species of Lepidoptera similarly fed inside the galls on the walls. They killed, and in a few cases partly ate, the *E. diana* larvae encountered, thus accidentally functioning as predators. The walls of the galls also were heavily mined and darkened by the small larvae of an unidentified species of *Liriomyza* (Diptera: Agromyzidae) (Figs. 1d, 1g), which apparently did not harm *E. diana* (Fig. 1g). Mining of gall walls by the *Apion* sp., *Liriomyza* sp., the torymid, and lepidopteran hastened gall decay and disintegration, in contrast to empty galls uninfested by inquilines that turned woody and persisted for several years (Benbow & Foster 1982).

The larvae of an unidentified clerid beetle were observed as predators of *E. diana* larvae and an adult was seen that had been freshly killed by a salticid spider. However, the more common predators of *E. diana* larvae and puparia were birds, which were especially active at the Mormon Rocks study site, where many galls bore open holes pecked by social, insectivorous bushtits, *Psaltriparus* sp. (Fig. 1h). Stoltzfus (1977) suggested that woodpeckers opened galls presumably formed by *E. longicornis* Snow on *Artemisia cana*.

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